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Studies on the oribatid mites of a Danish beech wood Soil[1])

I. Nutritional biology

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With 4 figures

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Contents

1. General introduction

It has been stated many times in the literature that, in view of their habits, nutrition, and large numbers, oribatid mites in woodland soil must have an important effect on the organic layers within which they mostly live. Few attempts have been made, however, to quantify this effect. This is no doubt due, at least in part, to our relative ignorance of the nutritional habits and requirements of this very diverse group of animals. There have been several general reports of observations on the feeding habits of oribatids, as well as a number of useful attempts to summarise this knowledge (Berthet 1964; Forsslund 1939; Hartenstein 1962a–g; Luxton 1966; Mignolet in press a, b; Noordam and van der Vaart-de Vlieger 1943; Pauly 1956; Rajski 1966; Riha 1951; Schuster 1956 van der Drift 1951; Wallwork 1958, 1967; Woodring 1963; Woolley 1960).

Schuster's work was of much value in that it prepared the ground for a nomenclatural framework with which to describe the feeding patterns of oribatid mites as a whole. Although it has been said (Clark 1968) that 'ecology has sometimes been defined as that branch of biology entirely abandoned to terminology', it nevertheless seems important to extend and stabilise this nomenclature in an early part of this paper. This is because I have come to believe that, although one cannot talk convincingly about the quantitative ecological influence of oribatid mites as a whole, one may be justified in doing so under headings which define their distinctive feeding habits.

1) Contribution from the Danish IBP, section PT.

The influence of oribatid mites on forest litter layers may also be assessed in terms of their digestive capabilities. Little attempt has been made to determine precisely which parts of their food are utilised, although it has generally been assumed that, of the material ingested, only the fungal and bacterial growths are digested. This paper accordingly reports a preliminary study of carbohydrase enzymes in oribatid mites which suggests that their digestive abilities are as wide-ranging as their ingestive abilities and that our ideas about their importance as decomposer agents must be much revised.

The smallness of most oribatid mites is a great hindrance to the detailed study of food quantities processed by them. Classical gravimetric methods of measuring intake, assimilation efficiency and ingestion rates are clumsy in relation to the body size of these animals, and are also difficult to apply to those foods often utilised by them. Consequently, there are few reports in the literature about successful quantitative measurements of food processing by mites, and these are nearly all of recent origin utilising radioisotopes as tracers and describing only one quantity in the production biology equation (BERTHET 1964; ENGELMANN 1961; KOWAL 1969). This report describes a pilot study of such a technique for measuring all parameters with a fungus-eating oribatid which seems to be potentially useful for future work.

This paper, then, is an attempt to synthesise and stabilise our knowledge about the nutritional biology of soil oribatid mites, to add further observations to those already in the literature on oribatid feeding specificity and requirements, to discuss the ecological importance of these observations, to assess some of the digestive capabilities of these animals, and to suggest a possible approach to the quantitative analysis of food processing by them, the better, ultimately, to estimate their overall influence in the forest soil system.

2. Research area

The oribatids were taken from the soil at one of the Danish IBP PT research sites. This was Hestehave wood, located on the shores of Kalø Vig near Rønde, north east Jutland. This woodland is a homogeneous stand of beech (*Fagus silvatica* L.), the trees being mostly about 90 years old. The soil is a slightly acid to neutral mull, and is covered in spring with a dense carpet of *Anemone nemorosa* L., and later by a more scattered vegetation of grasses (primarily *Melica uniflora* RETZ., and *Carex silvatica* HUDS.) and other herbs (e. g. *Oxalis acetosella* L., *Asperula odorata* L., and *Ficaria verna* HUDS.). The experimental animals were extracted from samples of beech litter and mineral soil by means of the conventional Tullgren funnel method.

3. Feeding habits

3.0. Introduction, review, and revised terminology

The Appendix summarises the current information found in the literature. SCHUSTER (1956) first used the terms "macrophytophage" and "microphytophage" to describe eaters of higher plant material and microflora respectively. The large group of general feeders he called "non-specialised". All oribatid mites may be classed under one or other of these broad headings, although they may display narrower preferences within them. Occasionally oribatids may also show a feeding habit which can be classed outside these groups, although this rarely appears to be more than casual.

A number of ecological parameters have been measured for the oribatid mite community of the Hestehave beech wood soil and, as will be shown in succeeding papers of this series, these parameters may often be associated rather well in terms of the broad feeding groups which have been separately ascertained for the mites. It may thus be possible to extrapolate these quantitative data to other communities, perhaps containing different species, once the broad range of their feeding habits is known. For ecological purposes, therefore, it may be valuable to discuss oribatid species in terms of at least the broad groups in the following framework:

A. Major feeding habits:

(3.1.) Macrophytophages — feeding strictly on higher plant material. (3.1.1.) Xylophages — feeding on woody tissue. (3.1.2.) Phyllophages — feeding on leaf tissue.

(3.2.) Microphytophages — feeding strictly on the microflora. (3.2.1.) Mycophages feeding on fungi and yeasts. (3.2.2.) Bacteriophages — feeding on bacteria. (3.2.3.) Phycophages — feeding on algae.

(3.3) Panphytophages — combining all or some of the sub-headings above, and having attributes of both main types.

B. Casual or incidental feeding habits:

(3.4.) Zoophages — feeding on living animal material.

(3.5.) Necrophages — feeding on carrion.

(3.6.) Coprophages — feeding on faecal material.

It requires numerous experiments from a variety of sources using a range of food materials before a species may be accurately allocated to one or other of the above broad groups. In the Appendix (chap 11) the species are separated into the two groups of fastidious feeders only where there us sufficient evidence to justify this. In the panphytophage group, however, superscripts are added according to the opinion of the authority, and some species will be seen to be, at best, uncertainly characterised. This strongly indicates that they are panphytophages with food preferences which lie outside the choices open to them in certain of the experiments. Wherever an author has indicated that an animal is a panphytophage this is allowed to override an account describing the species as a more specialised feeder. Moreover, if the evidence of a feeding group has not arisen from a choice experiment, the species in question has been associated with others of its genus or family. In other words, wherever, there is any significant uncertainty about the placing of a species in this scheme it has been assigned to the panphytophage list with a superscript indicating any difference of opinion.

3.1. Macrophytophages

As a general rule it can be said that the Phthiracaroidea are strictly macrophytophagous (Appendix), and feed on the decaying parts of higher plants. Occasionally, from analysis of gut contents as well as from laboratory observation, macrophytophagous oribatids have been thought to ingest fungal material too (Forsslund 1939; Hartenstein 1962a), but this is rare and probably results from starvation. Certain species in this feeding group can show a preference for the leaves of a particular type of tree (Berthet 1964; Murphy 1952, 1953), or for a particular stage in the decay of leaves (Hayes 1963; Wallwork 1958), or for a particular part of a higher plant (Wallwork 1958).

Most of the species in this group may be described as "phyllophages" since they consume the decaying leaf lamina of the plant, ultimately reducing the leaf to a skeleton. Jacot (1939) describes how the juveniles of a species of *Steganacarus* hollow out spruce needles leaving the space within the epidermis packed with faecal material. However, the careful observations of Wallwork (1958, 1967), among others, have shown that a number of species are "xylophages" consuming various parts of the woody tissue. In particular Wallwork mentions *Phthiracarus borealis* (Trägårdh) and the nymphs of *Hermannia* sp. as feeding on the woody vascular elements of leaves, whereas the adults and juveniles of species such as *Steganacarus magnus* (Nicolet) and *Euphthiracarus arduus* (C. L. Koch) may burrow into twigs. It is doubtful that many of these macrophytophagous species are confined to a wood diet. For instance, unlike Wallwork, Hayes (1963) observed little wood tunneling on the part of *S. magnus* or *E. arduus* but rather their excavation of numerous pits in the leaf mesophyll. However, certain species may be obligatory xylophages for particular stages in their life-cycle.

Little is known of the influence of oribatid mites on the underground parts of higher plants, but Woodring (1965) mentions *Rostrozetes flavus* Woodring as showing a distinct preference for the decomposing outer sheaths of roots.

Generally speaking, the macrophytophagous oribatids require their food to be somewhat softened and decayed by fungi before they will consume it (Hayes 1963; Jacot 1939; Murphy 1953). The food often also needs to be moist, although a species of *Achipteria*, of *Eupelops* and of *Peloribates* have been observed feeding on dry leaves (Kühnelt 1961; Wallwork 1967). Of the twenty oribatid species studied by Hartenstein (1962a)

none fed on any fresh wood, needle or leaf tissue presented, and the three phthiracarid species tested by HAYES (1963) fed to only a slight extent on fresh leaves or fresh litter. However, WOODRING (1963) has reported observing *Scheloribates laevigatus* (C. L. KOCH) feeding on fresh green grass in the laboratory, even though this diet could not sustain the culture. WALLWORK (1965) has described a galumnoid mite from Uruguay dwelling (at least in the nymphal stage) in burrows in the living parenchyma of the leaves of the water hyacinth (*Eichhornia crassipes*) which might also have formed the sole source of its diet. The consumption of fresh higher-plant material, however, appears to be exceptional.

3.2. Microphytophages

The most important oribatid groups appearing to be wholly microphytophagous are the Damaeoidea, the Oppioidea, and possibly the Eremaeoidea. Most will browse haphazardly on a wide range of fungi, yeasts, bacteria and algae although some show distinct preferences for one or other of these organisms. Sometimes they will even select specific parts of their microbial food, for WALLWORK (1958) and FARAHAT (1966) have reported that fungal spores are commonly found packing the guts of *Oppia neerlandica* (OUDEMANS) and *O. nitens* C. L. KOCH respectively. All members of the group can be described as "mycophages", although very few as "bacteriophages". In my laboratory cultures *Gustavia microcephala* (NICOLET) preferred to eat bacteria, although SCHUSTER (1956) found that this species would also eat fungal spores. The adults and juveniles of *Hypochthonius rufulus* C. L. KOCH, although also consuming fungi and yeasts, appear to have a predilection for bacteria. If this is a reflection of a natural habit, it might explain the "apparent absence of solid food" in the gut of *Hypochthonius* which was noted by WALLWORK (1967). The juveniles (but not the adults) of *Belba corynopus* (HERMANN) also readily accept a bacterial diet. Soil bacteria would be easily available to these forms since they mostly grow in sheets or clumps on soil crumbs (ALEXANDER and JACKSON 1954; HARRIS 1972; JONES and MOLLISON 1948).

So far as is known no oribatid is strictly "phycophagous". TARRAS-WAHLBERG (1961) writes that, at the surface of the Swedish mire which he was studying, algae were probably a food source for oribatids, and indeed *Nothrus pratensis* SELLNICK preferred *Protococcus* when this was offered. SENGBUSCH (1954) states that the juveniles of *Galumna confusa* WOODRING appear to need the algae *Protococcus* for their proper development, and has since had much success in rearing other oribatid species on this diet (SENGBUSCH and SENGBUSCH 1970). LUXTON (1966) notes that the littoral oribatid *Hygroribates schneideri* (OUDEMANS) will readily consume filamentous green algae as well as fungi, and that *Ameronothrus* sp. will browse on algal sporelings in and around barnacle growths. LITTLEWOOD (1969) has successfully kept eight species of oribatid in the laboratory on a diet of "algal scrapings from bark".

3.3. Panphytophages

The large majority of oribatid mites may belong to this group. Whereas the macrophytophages are characterised as never electing to browse on microbial growths, and the microphytophages as never comminuting higher plant material (even trough there may be a certain selectivity within these broad groups) the panphytophages may range widely through a broad selection of food materials available to them in their environment. Even here there may be some selectivity. Some may prefer to consume dead leaf material, although readily eating and thriving on microbial growths if no leaf material is available, and vice versa. This catholic feeding habit is ecologically of great advantage to the species possessing it since it may then support populations in a variety of habitats, with only the relative importance of a particular food component varying with locality. BERTHET (1964), for instance, indicates that the panphytophage *Xenillus* will not consume leaf

material from oak, hornbeam, beech or birch whereas in this Danish woodland *Xenillus* was one of the main beech-leaf skeletonisers. Moreover, MIGNOLET (in press, a) reports that *Nothrus palustris* C. L. KOCH refused all potential fungal foods but was strictly macrophytophagous. My own experiments with this species indicate that it will consume only small amounts of beech leaf but will readily eat a wide range of fungi and yeasts. These discrepances indicate that much care must be taken before a species can with confidence be assigned to any particular group.

3.4. Zoophages

Oribatids have, from time to time, been observed to feed on living animal material. The best-documented case is that described by ROCKETT and WOODRING (1966a, b) who observed all the stages except the larvae of *Pergalumna omniphagous* ROCKETT and WOODRING feeding upon live nematodes. Moreover, these authors maintain that the oribatid preferred to eat nematodes rather than the ground mushroom which formed its normal diet in culture. It was suggested by ROCKETT and WOODRING that nematode-eating oribatids might be useful in soil nematode control since, unlike other predators which might be highly selective, the oribatid populations would not be strictly dependent on the population density of the prey.

WOODRING (1963) cites the observation of GRAVES (1960) that a "*Galumna*" sp. fed on the living body of a fly larva, and of VITZTHUM (1943) that *Scheloribates laevigatus* was able to feed on the pupae of a parasitic hymenopteran. These appear to be isolated observations, and WOODRING has explained that of VITZTHUM by the fact that the mites perhaps accidentally ate into the pupa whilst feeding upon the decaying organic matter surrounding it. On the whole, oribatid mites are not well-designed for the predatory mode, being mostly well-armoured and slow-moving.

A number of species appear to be able to ingest the eggs of anoplocephalid cestodes (FREEMAN 1952; KRULL 1939; STUNKARD 1937; WALLWORK 1967) which are occasionally swallowed whole and may complete their development within the mite. Certainly some oribatid mites are known to be the intermediate host in the transmission of certain tapeworm infections, and BULANOVA-ZACHVATKINA (1967) provides a list of 54 species which are associated in this way with one or more of 13 species of parasite.

3.5. Necrophages

Most observers have noticed that oribatids in Berlese funnel extracts of living material will occasionally feed on the dead bodies of other small arthropods. This is usually only a random occurrence depending on circumstance (such as starvation), and has only once been reported as a preferred habit [WALLWORK (1958) for the nymphs of *Fuscozetes fuscipes* (C. L. KOCH)]. HARTENSTEIN (1962a) in his study of the food preferences of 20 oribatid species remarked that they never fed on dead mites or Collembola in his experiments. RIHA (1951) notes that *Hypochthonius rufulus* and *Metabelba pulverulenta* (C. L. KOCH) will feed on carrion under starvation conditions, and WALLWORK (1958, 1967) mentions *Peloribates* sp., *H. rufulus*, *Belba* spp., and *Liochthonius* spp. in this regard. My own observations showed that *Hemileius initialis* (BERLESE) was a frequent feeder on the dead bodies of Collembola. WOODRING (1965) notes that *Scheloribates parabilis* WOODRING fed on powdered cricket flesh, although his cultures did not thrive on this food.

The presence of dead bodies of large animals on the soil surface tends to repel oribatid mites (as indeed it does most of the soil fauna) from some distance beneath it during and for some time after the putrefaction stage, and BORNEMISSZA (1957) showed that the soil fauna played only a minor part in its decomposition.

3.6. Coprophages

A number of oribatids may be coprophagous, and WALLWORK (1967) suggests that the habit may be a common one amongst the immature forms of the wood tunneling species. For them, presumably, it is advantageous to be able to consume ready-comminuted material in this restricted environment until they achieve the adult ability to masticate decaying wood. WALLWORK's 1958 paper shows that a number of oribatids, including an *Oppia* sp. and *Galumna formicarius* (BERLESE), may have been obligate coprophages upon the faecal material of wood borers. *Scheloribates laevigatus* is also probably coprophagous but, as can be seen from the Appendix (chapt. 11), it is not obligatorily so and, indeed, most oribatids found to feed on faeces are probably readily classed as panphytophages.

4. Feeding specificity

4.0. Introduction

It has already been shown that oribatid mites may make broad choices between the food materials available to them within their habitats. The range of such food substrates is wide, and may originate from several floral species. It is of ecological interest to know whether these soil animals have finer grades of preference, since these will, to a large degree, influence their distribution patterns and the range of habitats which they will colonise. In practice it is difficult to find out of such preferences in fact exist because direct observation is almost impossible in view of both the small size of the animals and the density of their environment, and because laboratory studies are necessarily somewhat artificial. Nevertheless, laboratory investigations have provided much useful information.

Of the macrophytophages, MURPHY (1952, 1953, 1955) and HAYES (1963), quoting an unpublished report of SPENCER, state that *Steganacarus magnus* showed a marked preference for broadleaved rather than coniferous forest litter, and for ash rather than birch leaves. BERTHET (1964) allowed this species to choose between four species of broadleaved litter and found that it preferred hornbeam or hazel, followed by beech and finally oak.

Phthiracarus borealis also preferred hornbeam, but took oak as second choice, followed by birch and beech. It should be noted, however, that this kind of choice by the adult macrophytophage may result from the foods available to it during its development, or prior to its use in the laboratory experiment.

The panphytophagous and microphytophagous oribatids show considerable selectivity towards microbial species, as has been shown by HARTENSTEIN (1962a), LUXTON (1966), MIGNOLET (in press, a), and ŠERIF (1971). Such preferences were also tested for these feeding groups from the Hestehave soils.

4.1. Methods

One may study feeding specificity by examining gut contents of animals brought in from the field, by noting the foods taken by animals in laboratory culture, or by plating out faecal material on agar plates and identifying the resultant microbial growths.

The first method is satisfactory only for finding out the broad feeding groups, since macerated leaf litter and comminuted microbial material is difficult to identify with precision. MIGNOLET (in press, a) has tried the last method which seems to work adequately for microphytophages since the fungal preferences of *Damaeus onustus* C. L. KOCH, when separately tested in the laboratory, correspond quite exactly with the fungal species previously grown from its faeces. However, the method was less than satisfactory for the panphytophage investigated.

The second approach was adopted for the present study. A representative range of fungi, yeasts, and bacteria, obtained from the soil of the research area, were plated out in pure culture in petri dishes containing either malt extract agar (fungi) or soil extract agar (bacteria). A small portion of each of these microbial growths was ranged at regular intervals around the perimeter of a culture dish containing the usual plaster of Paris/charcoal substrate, and numbers of indivi-

duals of the particular mite species under study liberated into the dish. These were kept at room temperature and observed at regular intervals over a period of some days. Notes were kept of (1) numbers of individuals on a particular food portion, (2) evidence of feeding marks on the food, (3) presence of eggs on or near the food, and (4) presence and numbers of faeces on or near the food. The last type of feeding evidence was considered to be the most reliable for assessing preferences.

4.2. Discussion

The two macrophytophages studied [*Steganacarus spinosus* (SELLNICK) and *S. magnus*] would consume none of the microbial material offered, although one specimen of the former species did appear to have black material, possibly *Phoma*, in the gut. *Gustavia microcephala* fed actively upon one bacterial culture (that noted as "spore-forming rods in chain formation"), with signs of feeding on the other three bacteria presented, and is therefore considered to be a bacteriophage. However, there is evidence that it may also have consumed some of the fungus *Zygorrhynchus* sp.

The results for the other microphytophages and the panphytophages are presented in Tables 1 and 2.

Feeding specifity experiments may contribute information concerning the distribution patterns of the oribatid mites in a vertical plane. In view of the fact that fluctuations in the mycofloras of woodland soil cannot be definitely regarded as seasonal (PARKINSON and BALASOORIYA 1969) it seems unlikely that these particular food specificities will seriously influence the seasonal periodicity of the oribatid populations.

A certain amount is known of the vertical distribution patterns and successions of the forest soil microflora (BURGES 1958, 1967; CHESTERS 1960; HAYES 1965a; HOGG and HUDSON 1966; HOLM and JENSEN in press; HUDSON 1968; JENSEN 1963, 1971; PARKINSON and BALASOORIYA 1969; PARKINSON and KENDRICK 1960; SAITO 1956; SMIT and WIERINGA 1953; RUSCOE 1971; WITKAMP 1960), and where such distributions are definitive it

Table 1 Feeding preferences of the microphytophagous oribatids from the beech wood soil

	Damaeus clavipes		*Belba corynopus*		*Hypochthonius rufulus*	
	adults	juveniles	adults	juveniles	adults	juveniles
"black sterile mycelium"	+	+	++	−	+++	++
Phoma sp.	+++	+	++	+	+++	++
Candida sp. 2 (MO-2)	+	+++	+	+++	+	+
yellow gram — ve motile rods (LII—1)	+?	+?	+?	+	+++	+
Streptomyces sp.	−	−	−	+++	+	++
"spore-forming rods in chain formation" (MII-13)	−	−	−	+	++	++
small gram + ve motile Vods (LII-50)	−	−	−	++	+++	+++
Candida sp. 1 (M-42)	+	−	−	+	+	+
Cryptococcus albidus	−	−	+	++	++	+++
Synsporium sp.	−	+	+	−	−	−
Trichoderma viride	+	+++	−	−	−	−
Sporobolomyces roseus	+	−	−	−	−	++
Rhodotorula sp.	−	+++	++	−	−	+
Torulopsis sp. 1 (M-6)	−	+	++	−	++	+
Aureobasidium pullulans	++	+	−	+++	−	+++
Zygorrhynchus sp.	++	−	++	+	−	++
Penicillium sp.	−	−	+++	−	−	−
Mucor sp.	−	−	−	−	+?	−
Beech leaf	−	−	−	−	−	−

+++ = primary preference; ++ = secondary preference; + = occasionally eaten; − = never eaten.

Table 2 Feeding preferences of the panphytophagous oribatids from the beech wood soil

	Adoristes ovatus	*Ceratozetes gracilis*	*Achipteria juveniles*	*Xenillus anasillus*	*Nothrus silvestris*	*Nothrus palustris*	*Nothrus juveniles*	*Hemileius initialis*	*Achipteria coleoptrata*	*Chamobates cuspidatus*
Beech leaf	++	++	+	+++	+++	+	+++	−?	+	+
"black sterile mycelium"	+++	+++	+	+++	+++	+++	−	+	+++	+++
Phoma sp.	+++	+	+ +	++	−	−	+++	++	+++	++
Aureobasidium pullulans	+	+	+++	+	−	++	++	−	++	−
Cryptococcus albidus	+++	+	+	+	+++	+++	++	+++	+++	−
Candida sp. 2 (MO-2)	+	+	++	++	+	−	+++	+	−	−
Candida sp. 1 (M-42)	+	+	+++	++	++	+	+++	++	−	−
Mucor sp.	+	+	+	+?	−	−	−	++	−	−
small gram + ve motile rods (LII-50)	−?	+	+	+	−	+	+?	−	−	−
Zygorrhynchus sp.	−	−	−	+?	+	−	+?	+++	+	−
Torulopsis sp. 1 (M-6)	+	−	−	−	+		−	+	−	−
Sporobolomyces roseus	−	−	+	−	−		++	−	−	−
"spore-forming rods in chain formation" (MII-13)	−	+?	−	−	+?		−	−	−	−
Rhodotorula sp.	−	−	+	+	+		++	−	−	−
Streptomyces sp.	−	+	++	−	−	−	−	−	−	−
yellow gram − ve motile rods (LII-1)	−	+	−	+	−	−	−	−	−	−
Trichoderma viride	−	−	−	+?	−	−	−	−	−	−
Synsporium sp.	−	−	−	−	+?	−	−	−	−	−
Penicillium sp.	−	−	−	−	−	−	−	−	−	−

+++ = primary preference; ++ = secondary preference; + = occasionally eaten: − = never eaten.

Table 3 Index of affinity between the microphytophagous oribatids on the basis of their feeding preferences

	H. rufulus juveniles	*Hypochthonius rufulus*	*B. corynopus* juveniles	*Damaeus clavipes*	*Belba corynopus*	*D. clavipes* juveniles
H. rufulus juveniles		*	*	*	—	—
Hypochthonius rufulus	800		*	—	—	—
B. corynopus juveniles	833	762		—	—	—
Damaeus clavipes	696	500	632		—	—
Belba corynopus	667	571	500	526		—
D. clavipes juveniles	609	500	421	667	737	

Numbers represent the index of affinity $\times 10^3$
* indicates a significant affinity at least at the 5% level of probability
— not significant

seems reasonable to assume that an oribatid with a distinct preference for that particular microbe will live in the same zone. Little is known of the precise distribution patterns of oribatids through the L, F, and H layers of the forest floor (ANDERSON and HEALEY 1970; AOKI 1967; HAARLØV 1955; HAYES 1965b; KÜHNELT 1961; LEBRUN 1965; VAN DER DRIFT 1951; WALLWORK 1970), but where information is available it is interesting to relate it both to the feeding preferences of the animals and to what is known of the distribution of the food substrates. Ultimately, using such techniques as those developed by HAARLØV and WEIS-FOGH (1953) and ANDERSON and HEALEY (1970), we shall have a more detailed indication of distribution patterns of oribatid mites, but for now only the following generalisations can be made. This information concerns only those species found in Hestehave wood and is culled from a number of sources. The larger forms such as *Steganacarus magnus*, *Damaeus clavipes* (HERMANN), *Adoristes ovatus* (C. L. KOCH) and *Achipteria coleoptrata* (LINNAEUS), as well as the much smaller *Chamobates cuspidatus* (MICHAEL), are more common in the surface litter (L) layer than in the deeper zones. The commonest fungi of this layer are *Phoma* sp., *Aureobasidium pullulans* (DE BARY) ARNAUD, and the "dark sterile mycelium". Table 1 shows that *Damaeus clavipes* has a preference for *Phoma* sp. as well as a subsidiary liking for *A. pullulans*. Table 2 shows even more clearly that *Adoristes ovatus*, *Achipteria coleoptrata*, and *Chamobates cuspidatus* have a distinct preference for those microbial species known to inhabit the litter layer.

The fauna of the upper mineral soil and the humus (H) layer are generally represented by small, weakly-sclerotised forms with little resistance to desiccation. They include *Hemileius initialis*, *Hypochthonius rufulus*, and many of the immature oribatids, and are said by KÜHNELT (1961) (who was quoting RIHA) to be mainly necrophagous forms. This part of the soil profile is by far the most richly endowed with bacteria (HOLM and JENSEN in press), and the animals from this region may have appeared to be necrophagous in laboratory culture because of their predilection for moist, bacteria-rich foods. *H. initialis* has already been noted as a necrophage, but it must also be said that in culture it would not take pure bacterial growths. The most noteworthy bacterial feeder was *Gustavia microcephala* (its long sickle-shaped mouthparts, serrated on one edge, are undoubtedly well-designed for scraping bacterial films from the substrate) and it is tempting to suggest that these lower organic horizons will be found to be its native habitat. *Hypochthonius rufulus*, both adults and juveniles, will take a wide range of food materials but are also keen feeders on bacterial films. This observation matches their known habitat preference. The juveniles of *Belba* are also closely associated with *Hypochthonius* in regard to preferred

Table 4 Index of affinity between the panphytophagous oribatids on the basis of their feeding preferences

	Adoristes ovatus	*Ceratozetes gracilis*	*A. coleoptrata* juveniles	*Xenillus anasillus*	*Nothrus juveniles*	*Hemileius initialis*	*Nothrus palustris*	*Nothrus silvestris*	*Achipteria coleoptrata*	*Chamobates cuspidatus*
Adoristes ovatus		*	*	*	—	*	—	—	—	—
Ceratozetes gracilis	818		*	*	—	—	—	—	—	—
A. coleoptrata juveniles	818	833		*	*	—	*	—	—	—
Xenillus anasillus	783	800	800		*	*	—	—	—	—
Nothrus juveniles	700	636	818	783		—	—	—	—	—
Hemileius initialis	842	667	667	727	632		—	—	—	—
Nothrus palustris	700	636	727	609	700	526		—	—	—
Nothrus silvestris	600	546	546	609	600	737	700		—	—
Achipteria coleoptrata	625	556	556	632	625	667	500	500		—
Chamobates cuspidatus	462	400	400	375	308	500	308	308	667	

Numbers represent the index of affinity $\times 10^3$
* indicates a significant affinity at least at the 5% level of probability
— not significant

food substrates (Table 3), and may therefore be found to inhabit preferentially the H layer. It is worth noting (Tables 1 and 2) that none of the oribatid species known to inhabit the drier surface layers of the litter will take a bacterial diet.

The "fermentation" zone (the F layer intermediate between the litter and the humus) contains a group of species that includes *Nothrus silvestris* NICOLET, and *Belba corynopus*. The lower layers of the organic fabrics are characterised by a greater development of such fungi as *Trichoderma viride* PERS., *Zygorrhynchus* sp., *Mucor* sp., and *Penicillium* sp. Yeasts are especially common in the F layer. *Belba corynopus* is noteworthy as the only oribatid species tested which will consume *Penicillium*, and some of its subsidiary preferences are for the fungus *Zygorrhynchus* and several yeasts. It is also probable that the juveniles of *Damaeus clavipes* inhabit these middle and lower zones since they have a decided preference for *Trichoderma viride*. *Nothrus silvestris* will not consume the surface-dwelling fungi *Phoma* and *Aureobasidium*, but will select a wide range of yeasts and may therefore be similarly confined to these middle layers. *Hemileius initialis*, noted in the literature as an inhabitant of the H layer, will consume *Mucor* and *Zygorrhynchus* and is almost certainly therefore an inhabitant of the lower organic layers, but it will also select a wide range of yeasts and probably dwells in both the F and H layers.

From the point of view of its food preferences, *Ceratozetes gracilis* (MICHAEL) almost certainly ranges widely through all the organic layers. *Xenillus anasillus* WOOLLEY and *Nothrus palustris* may also do this, but on balance both appear to prefer to remain in the L and F layers, which would be expected in view of their large body size. The association analysis (Fager's index) between the panphytophagous oribatids (Table 4) indicates a strong affinity between *Adoristes ovatus*, *Ceratozetes gracilis*, *Achipteria coleoptrata* juveniles and *Xenillus anasillus* on the basis of food materials taken by them. This is no doubt brought about since these four species each consume the widest variety of food materials, and it may therefore be an indication that this group is the one most significantly able to utilise all zones of the organic horizons.

KÜHNELT (1961), SENGBUSCH (1954), WALLWORK (1958), and WOODRING and COOK (1962) have clearly shown that immature stages often require different foods from their adults. WOODRING (1963) suggests that this holds good for the pterogasterine species since all the apterogasterine species cultured by him fed on the same food in all stages.

Table 5 Possible distribution in a vertical plane of some woodland soil oribatids, according to their food preferences

Soil layer	Microbial species	Oribatid species			
Litter (L)	*Phoma* sp. *Aureobasidium pullulans* "Dark sterile mycelium"	*Chamobates cuspidatus* *Damaeus clavipes* *Adoristes ovatus* *Achipteria coleoptrata*		*Xenillus anasillus* *Nothrus palustris* *Achipteria* juv. *Nothrus* spp. juvs.	*Ceratozetes gracilis*
"Fermentation" (F)	Yeasts *Zygorrhynchus* sp. *Mucor* sp.	*Hemileius initialis*	*Nothrus silvestris* *Belba corynopus* *Damaeus* juvs.		
Humus (H)	*Trichoderma viride* *Penicillium* sp.				
Mineral soil	Bacteria	*Hypochthonius rufulus* *H. rufulus* juvs. *Belba corynopus* juvs. *Gustavia microcephala*			

However, LUXTON (1966), investigating more precise responses to food materials from the natural habitat of *Hermannia pulchella* WILLMANN, found that the juveniles of this apterogasterine form also fed for preference upon different fungal species from the adult. Indeed, there was evidence of a different fungal food material being selected for each of the developmental stages. Clearly the wider the range of natural food materials made available to oribatid mites throughout their development, the more selective they appear to be.

A few of the Hestehave species were also represented in the food selection experiments by their immatures. In only one case (*Hypochthonius rufulus*) could the adults and juveniles of the same species be associated together on the basis of their food preferences. That this different selection of food material by the juvenile is not simply fortuitous has ben shown by HARTENSTEIN (1962 b, c). In his experiments with *Belba kingi* HARTENSTEIN the juveniles developed most rapidly when confined to a diet of *Trichoderma*. When attempts were made to rear this species on other foods known to be selected by the adult, development did not proceed beyond the larval stage. Indeed, if the immatures are distributed in the organic horizons according to their food preference (Table 5), they almost always inhabit that layer below the one preferred by their parents, and this confirms an impression from field sampling by VAN DER DRIFT (1951). This pattern of preference would seem to be of great ecological advantage since the adults and their immatures would not then be competing for either food resources or living space.

All of this somewhat circumstantial evidence is summarised in Table 5.

5. Carbohydrase enzymes in soil oribatids

5.0. Introduction

Some members of the soil fauna are able to assist directly in the breakdown of dead plant material by digesting certain plant structural polysaccharides either through the possession of the necessary enzymes, or a symbiotic gut flora (NIELSEN 1962). Such ani-

mals include slugs and snails, tipulid larvae, termites, some nematodes, and some lumbricid earthworms. Soil oribatids, on the other hand, have generally been presumed to play a less direct role in the breakdown of decaying higher plant material, and even the macrophytophages were considered to utilise only the microbial growths on the organic matter ingested (NIELSEN 1962; WALLWORK 1967). This hypothesis was given credence by the experiments of HARTENSTEIN (1962f) who showed that *Protoribates lophotrichus* (BERLESE) fed vigorously on dead leaf tissue until the microorganisms within it were destroyed either by heating or by treatment with fungicide. WOODRING and COOK (1962) showed that the larvae of the panphytophage *Ceratozetes cisalpinus* WOODRING and COOK, hatched from surface-sterilised eggs, required the presence of fungal hyphae before they could feed on other aseptic food. LITTLEWOOD (1969) perfected techniques for surface sterilisation of oribatid mites, and showed that when sterile mites were provided with food (in this case algal growths from tree bark) which was free from bacteria and fungi no feeding occurred. That this was not due to the surface sterilising procedure was obvious when the animals began almost immediately to feed when presented with unsterilised bark scrapings. Littlewood suggests that food is not recognised as such by the oribatids unless microorganisms are present on it, or alternatively that the microorganisms might affect the food in some way (perhaps by beginning its breakdown) which makes it palatable to the mites. HAYES (1963) has also posed the question of whether fungus infection of organic matter is a necessary mechanical precursor to burrowing activity by the macrophytophages, or alternatively whether it is a necessary constituent of the diet.

There is little information concerning the digestive capabilities of oribatid mites which might be used to assess their biochemical efficiency in converting dead organic matter, or to assess qualitatively that part of their diet which they might utilise. NIELSEN (1962), in his extensive investigation of the carbohydrase enzymes of soil invertebrates, did not analyse oribatid mites. However, since oribatids consume mainly plant materials it would be ecologically instructive to be able to tabulate the carbohydrases in their digestive tracts. KÜHNELT (1961) intriguingly states that "decomposition of organic residues in the gut of the oribatid proceeds quite a long way and scarcely any cellulose residues remain", but does not present analytical evidence for this remark. SCHUSTER (1956) suggests that much of the material ingested by oribatids leaves the gut largely unchanged. However, GASDORF and GOODNIGHT (1963) have demonstrated proportionate increases in lignin and decreases in cellulose in the faeces of oribatid mites (*Peloribates* sp. and *Hermanniella* sp.) feeding on oak litter. SPAIN and LUXTON (1971) have indicated that certain oribatids can digest cellulose and other plant polysaccharides, and ZINKLER (in press) notes the presence of a cellulase in some species.

A preliminary investigation of carbohydrase enzymes was undertaken for a wide range of the Hestehave oribatids, in order both to complement the other nutritional biology investigations and to clarify the ecological influences of oribatid digestive capabilities.

5.1. Methods

Live oribatids (in numbers according to their physical dimensions) were homogenised in citric acid/phosphate buffer. For *Steganacarus magnus*, *Damaeus*, *Belba*, *Xenillus*, *Nothrus palustris* and *N. silvestris*, fifty individuals/cc of buffer was found to provide a sufficient concentration, whereas for *Damaeus* juveniles, *Nothrus* juveniles, *Hypochthonius*, *Ceratozetes*, *Achipteria*, *Hemileius*, and *Adoristes* 100 individuals/cc were required, and for *Steganacarus spinosus* some 200 individuals/cc. The homogenate was centrifuged for ten minutes at about 2000 G, and 50 μl of the clear supernatant liquid pipetted into individual round-bottomed digestion tubes. The pH of the citric acid/phosphate buffer used to make the homogenates was generally 6.1, except when the analysis was for cellobiase (5.2), cellulase (5.6), or pectinase (6.6). 50 μl of the relevant substrate were added to each tube, except in the case of pectin, xylan, chitin and microcrystalline cellulose when a small quantity of dry material was used. One tube in each series was always left with homogenate + buffer only as control. A drop of toluene was added to each tube as a

bacteriostatic agent, the tubes sealed with parafilm, and placed in an incubator at 37 °C for about 48 hours. The material was then spotted onto Merck Kieselgur F254 plates (together with control spots of all the potential end-products of hydrolysis), and the separation of any products of hydrolysis was performed with a solvent of ethyl acetate and 65 % 2-propanol (2 : 1). After drying the plates were sprayed with a mixture of 95 % ethanol, concentrated sulphuric acid, and anisaldehyde (18 : 1 : 1), and developed in an oven at 100 °C. The products of hydrolysis were recognised by their characteristic positions and/or colours. At least two incubations were made of each enzyme/substrate with at least two spottings from each. Often, especially when in doubt, many more incubations were made.

5.2. Discussion

The results of these analyses are set out in Table 6, and subdivided according to the main feeding groups to which the oribatids belong. The animals as a whole appear to possess a wide range of carbohydrase enzymes, the presence or absence of which is somewhat variable between species. Of the fifteen enzymes analysed, the only ones which are constantly present in all twelve species tested are the α-glucosidase maltase, and the β-glucosidase cellobiase; the only ones constantly absent are the β-galactosidase lactase, and galactanase.

Perhaps the most interesting result of these experiments is that enzymes capable of digesting some of the more complex polysaccharides are recorded and, amongst the macrophytophages and the panphytophages, a cellulase is generally accompanied by a xylanase and a pectinase. Nielsen (1962) has stated that this combination of enzymes may be taken as an indication that the animals possessing them are able to decompose plant structural polysaccharides as they occur naturally in litter, wood and other plant remains. These remains are complex substances with the assimilable saccharides no doubt masked by indigestible substances such as lignin and suberin. However, macrophytophagous oribatids macerate dead leaf tissue to a very great extent, thus presumably uncovering digestible surfaces, and they also process much material during the course of their feeding.

The method of enzyme analysis used does not, of course, distinguish between enzymes produced by the animals themselves and those produced by a symbiotic gut flora. Ecologically the origin of these enzymes is of no great moment, but it is interesting to speculate. Hartenstein (1962f) was unable to demonstrate conclusively the presence of a symbiotic gut flora in a panphytophagous oribatid, but Woodring (1963) found some yeastlike organisms in the midgut and lateral caecae in almost 100 % of the investigated adult specimens of *Galumna confusa*. Engelmann (1961), quoting an unpublished report by Rohde, says that the digestive tract of adult *Pseudotritia* is filled with rod-shaped bacteria. Haarløv (pers. comm.) has also noted proventricular caecae in *Platynothrus peltifer* (C. L. Koch) which may have contained a symbiotic flora. These gut organisms have not been properly identified or their effect on nutrition ascertained, so that a solution to this problem must await investigations on enzyme histochemistry.

The microphytophages are certainly able to digest one polysaccharide, amylose, and may additionally be able to break down a second, chitin. The chitin used in these experiments was in the form of pure flakes the hydrolysis of which, if it occurred, was no doubt slow and with the production of only small amounts of end-product. This is probably the reason for the mass of queries in the chitinase column of Table 6. It is probably significant, though, that all the microphytophages are noted as having a potential for chitin digestion since Cochrane (1958) notes that the cell walls of fungi contain a high proportion of chitin, probably in the form of microfibrils lending structural rigidity. Burnett (1968) showed that *Mucor* has approximately 10 % chitin in the cell wall, and a chitinase may therefore be advantageous for lysing the cell walls prior to the digestion of the contents. Burnett has also stated that the *Mucor* cell wall contains 33 % chitosan, 6 % protein, and 8 % lipid and, although it would seem that enzymes such as lipase and phosphatases

Table 6 Carbohydrase enzymes in oribatid mites

	Macrophyt		Panphytophages								Microphytophages			
	Steganacarus magnus	*Steganacarus spinosus*	*Achipteria coleoptrata*	*Hemilelus initialis*	*Adoristes ovatus*	*Xenillus anasillus*	*Ceratozetes gracilis*	*Nothrus palustris*	*Nothrus silvestris*	*Nothrus juveniles*	*Belba corynopus*	*Damaeus clavipes*	*Damaeus juveniles*	*Hypochthonius rufulus*
α-glucosides														
Maltose	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sucrose	+	−	+	+	+	+	+	+	+	+	+	+	+	+
Melezitose	−	?	−	−	?	+	+	+	+	+	+	+	+	−
Trehalose	−	−	−	+	?	+	+	+	+	+	+	+	+	+
β-glucosides														
Cellobiose	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Salicin	+	+	+	+	+	+	+	+	+	+	+	−	+	+
α-galactosides														
Raffinose	?	?	+	+	+	+	+	+	+	+	+	+	+	+
Melibiose	+	+	+	+	+	+	+	+	+	+	−	−	−	−
β-galactosides														
Lactose	−	−	−	−	−	−	−	−	−	−	−	−	−	−
polysaccharides														
Amylose	?	+	?	−	?	+	+	+	+	+	+	?	+	+
Cellulose	+	+	+	+	+	+	+	+	+	+	−	−	−	−
Pectin	+	+	+	?	?	+	+	+	+	+	−	−	−	−
Xylan	+	+	+	+	+	+	+	+	+	+	−	−	−	−
Chitin	?	−	−	+	−	−	?	?	?	−	?	?	?	?
Galactan	−	−	−	−	−	−	−	−	−	−	−	−	−	−

Note: + = positive reaction, − = negative reaction, ? = not certain.

could also therefore serve to lyse the cell wall, PHAFF (1971) indicates that they have no such effect on the cell walls of yeasts.

According to NORTHCOTE (1963) yeasts contain three polysaccharides as distinct entities. These are the storage material glycogen, and the structural components glucan (which is highly insoluble) and mannan (which is a very soluble polysaccharide). MANNERS (1971) adds trehalose as one of the reserve carbohydrates of yeast, and states that 40% of the dry weight of anaerobically grown yeast cells may be in the form of reserve carbohydrate. Trehalose is sparsely found in higher plants, but COCHRANE (1958) points out that it is the only disaccharide to be formed free in appreciable amounts by fungi. Amylase is commonly possessed by oribatid mites but, interestingly, trehalase was found only in those animals which included a wide range of fungi in their diet. Neither it nor melezitase was analysed from the macrophytophage homogenates, perhaps an indication that they do not, after all, digest much of the random fungal growths on their main diet. C. O. NIELSEN (1962) was unable to detect a melezitase in enchytraeid worms, and this enzyme was absent or only weakly present in the enchytraeids tested by B. O. NIELSEN (1966). It is perhaps more illuminating in this context that NIELSEN (1962) was also not able to find a trehalase in earthworms which, like macrophytophagous oribatids, are also feeders upon decaying organic matter.

The table further indicates the probable absence of a raffinase from the macrophytophages but the presence of a melibiase, with the reverse situation occurring in the microphytophages. This is curious since the two sugars are closely related and raffinose may, in any event, be hydrolysed to melibiose and fructose by sucrase (COCHRANE 1958). Perhaps it is significant that a sucrase does not appear to be present in *Steganacarus spinosus*. Melibiose is not utilisable by many fungi and therefore possibly of no importance to purely fungal feeders who have not, in consequence, evolved an enzyme capable of handling it. This seems to be commonplace among fungal-feeding soil animals since ZINKLER (1968) showed the absence of melibiase from two of three Collembola species tested, with only weak activity in the third.

To a certain extent the pattern of carbohydrase enzymes seen in the panphytophages matches the feeding habit of the various species within this group. For instance, *Achipteria coleoptrata* is a somewhat restricted feeder, eating relatively few of the foods presented to it, and its complement of carbohydrase enzymes is similarly reduced. For reasons which are not clear, *Achipteria*, *Adoristes*, and *Hemileius* are closer to the macrophytophage group on the basis of their enzyme complements than to any of their fellow panphytophages or to the microphytophages.

6. Measurements of ingestion, assimilation, and egestion rates

6.0. Introduction

A number of qualitative observations have appeared in the literature dealing mainly with feeding rates compared between species or between immature stages. Most authors have agreed that the immatures are the most important feeding stages, and that they feed continuously (WALLWORK 1967; WOODRING 1963). The feeding rates of the different stages, however, may not be constant throughout the life-cycle, and the tritonymph appears to be that stage found to process the most material. Thus, MURPHY and JALIL (1964) found that some 30% of the tritonymphs in their field populations of *Tectocepheus velatus* (MICHAEL) had food in the gut compared with 17—20% of the adults and other juveniles. ROCKETT and WOODRING (1966b) have also remarked that, of the immatures of their species *Ceratozetes jeweli* ROCKETT and WOODRING, the tritonymphs appeared

to be "the heaviest eaters". WALLWORK (1967) emphasises the probable significance of the feeding habits of later nymphal stages. WOODRING (1963) also notes that young adults feed voraciously, but that the amount of food consumed decreases with increasing age. This seems to occur more rapidly in some species than in others. Thus *Rostrozetes flavus* and *Oppia nova* (OUDEMANS) adults continue to feed for almost their entire life, but the more "advanced" oribatids like *Galumna confusa*, *Scheloribates laevigatus* and *Ceratozetes cisalpinus* cease feeding almost entirely after only two or three weeks of adulthood.

BERTHET (1964, ENGELMANN (1961), HARTENSTEIN (1962e and f), KOWAL (1969) and MURPHY (1952, 1953) have, to a greater or lesser degree, attempted to quantify food processing in oribatid mites. In no case is the information complete or adequate. BERTHET, HARTENSTEIN, and MURPHY have estimated egestion rates for certain species, as well as food residence time in the gut, although only BERTHET provides figures for mass egested. BERTHET, KOWAL, and MURPHY provide useful figures for ingestion rates and quantities, and BERTHET also estimates the assimilation efficiency of *S. magnus*. ENGELMANN, in a classic paper, estimates intake, assimilation, and egestion for a whole field population of oribatids.

6.1. Methods

Classical gravimetric methods of measuring consumption and egestion (and, by difference, assimilation) are inadequate for most oribatid mites in view of their small body size and the minute amounts of food which they take. These methods become even more untrustworthy for the microphytophagous forms and, although tried at the Mols Laboratory, were soon abandoned because of the difficulties inherent in weighing tiny portions of living fungal food material. Instead it was decided to embark upon the kind of radiotracer technique used with such success for other animals by HUBBELL, SIKORA, and PARIS (1965), PARIS and SIKORA (1967), REICHLE (1967), and WILLIAMS and REICHLE (1968).

The use of radioisotopes to measure quantities in the production biology equation is not unknown for oribatid mites (BERTHET 1964; ENGELMANN 1961; KOWAL 1969; MCBRAYER and REICHLE 1971) but in no case has it yet provided complete details for any particular species.

Assimilation rates may be measured by allowing an animal to feed on radioactively contaminated food, then transferring it to uncontaminated food and measuring the elimination of radioisotope over a period of time (REICHLE 1967). This allows the plotting of an elimination (sometimes called a retention) curve which is usually of the two-component type (Figs. 1—4). This sort of curve shows a rapid initial loss of radioisotope material due to egestion of unassimilated radioisotope from the gut. Loss through the second component takes place over a longer period of time and represents the excretion of assimilated material. An estimate of the proportion of radioisotope

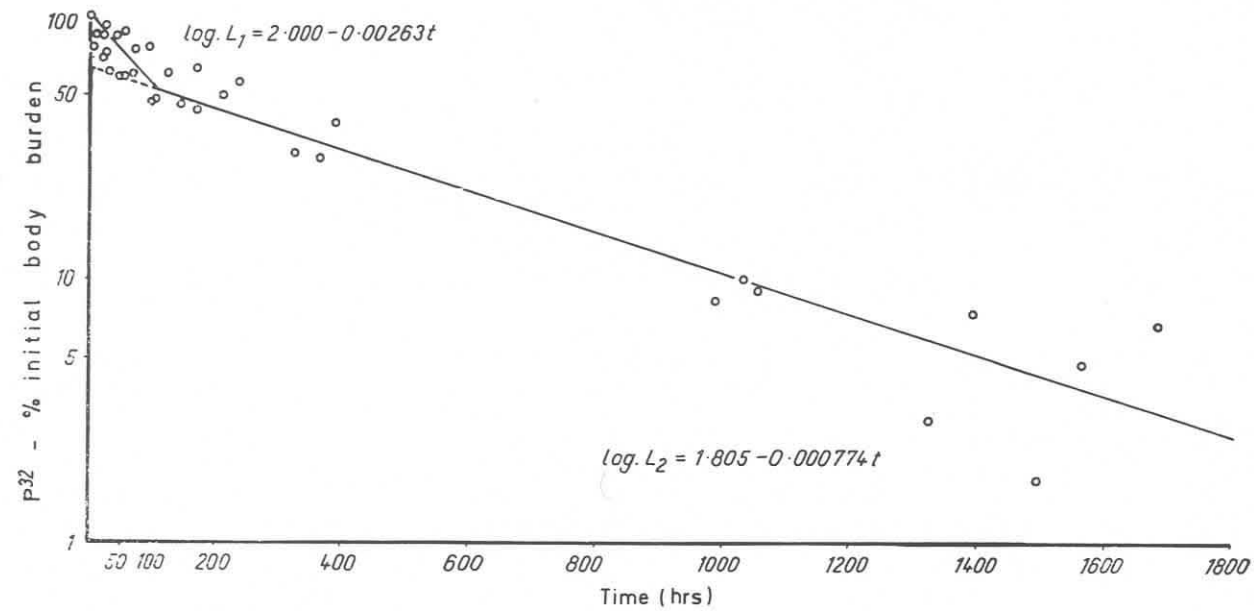

Fig. 1. Radioisotope elimination curve for *Damaeus clavipes*, adults.

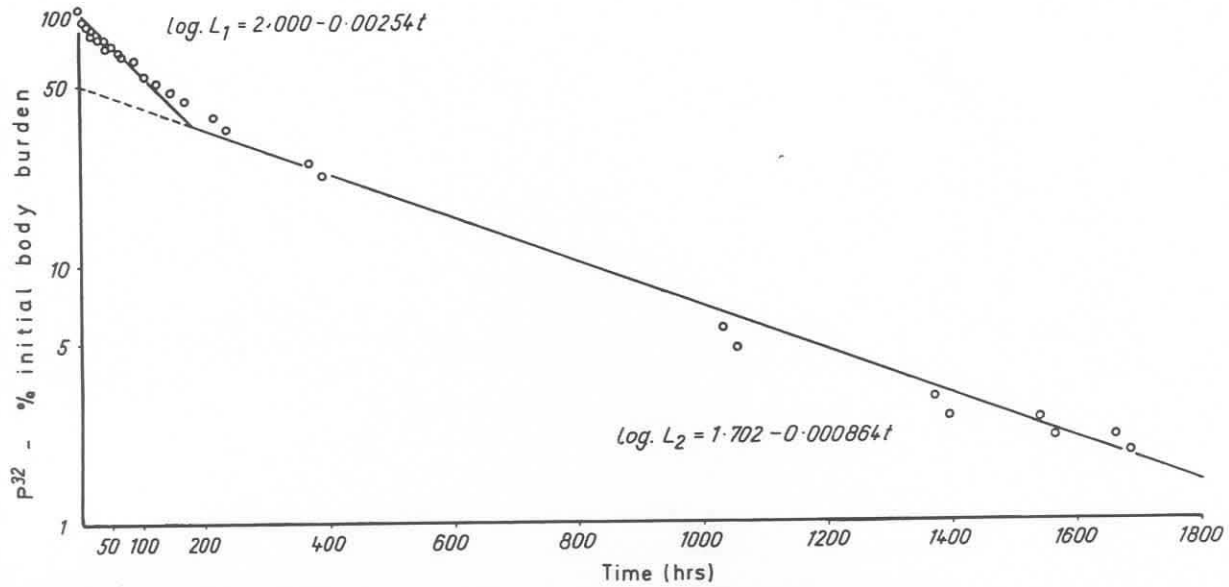

Fig. 2. Radioisotope elimination curve for *Damaeus clavipes* tritonymphs.

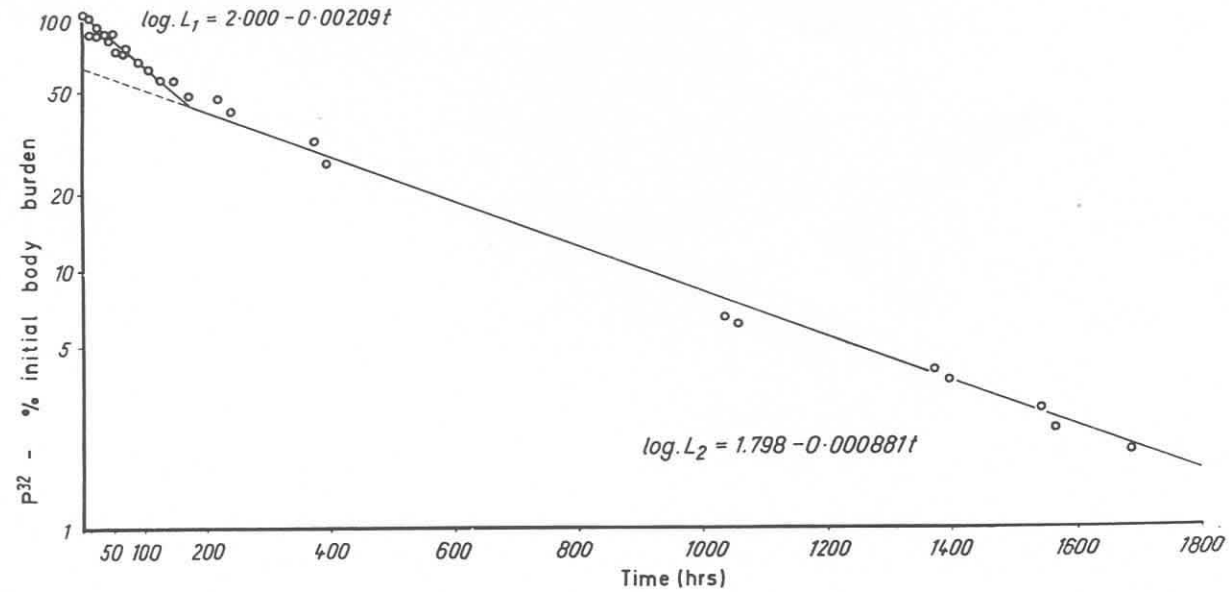

Fig. 3. Radioisotope elimination curve for *Damaeus clavipes*, deutonymphs.

assimilated may thus be made by extending the assimilation component line back to time 0. This may be converted to the actual proportion of food material assimilated by the method of Hubbell, Sikora and Paris (1965):

$$\text{Fraction assimilated} = \frac{\text{proportion of radioisotope assimilated} + \text{activity of mites}}{\text{activity of ingested food}}$$

A simple estimate of ingestion rate was made by feeding animals upon radioactive food of known specific activity for 24 hours, and then measuring then radioisotope uptake by the body. This can readily be converted to mass of food consumed from the specific activity data.

Both types of measurement were made for the protonymphs, deutonymphs, tritonymphs and adults of *Damaeus clavipes* using P^{32} as the radio-source. For radioactivity measurements a Phillips counter/ratemeter was employed, with an automatic sample-changer and printout. During the counting the live animals were contained in small holes drilled in the centre of the moist plaster of Paris/charcoal mixture which filled the usual sample planchettes. This was in order to minimise potential errors from inconstant geometry. The animals were confined to the hole by a barrier of opaque scotch tape. All experiments were performed at 15 °C, and the animals were fed upon known preferred fungi. This was *Trichoderma viride* in the case of the juvenile

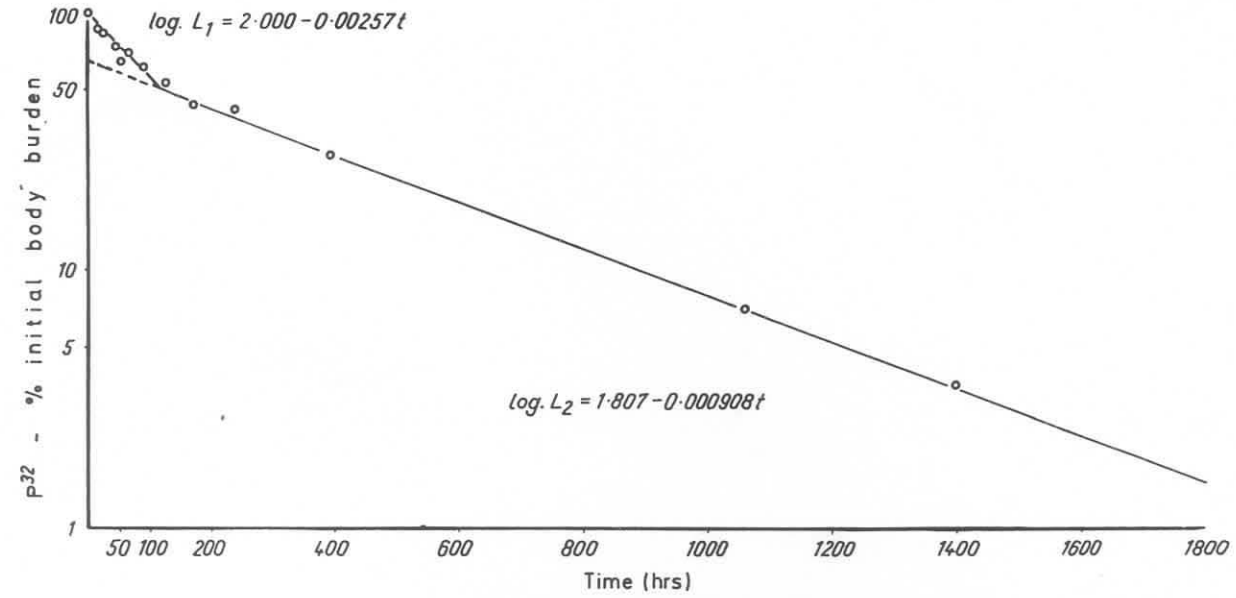

Fig. 4. Radioisotope elimination curve for *Damaeus clavipes*, protonymphs.

stages, and *Phoma* sp. for the adults. The mean calorific values (as measured with the Phillipson microbomb calorimeter) for these fungi were: *T. viride*, 4774 cals/g substrate; *Phoma* sp. 4598 cals/g substrate. The radioisotope was introduced onto the food by harvesting the mycelium from an agar plate and mixing it thoroughly with P^{32} (orthophosphate) solution, thereafter allowing it to dry somewhat to minimise surface contamination effects. This procedure seemed not to affect the palatability of the fungus to the mites, and gave rise to a remarkably even specific activity of the food portions.

Phosphorus is probably not the ideal element for use in such studies since the animals (and especially the juveniles) presumably have a strong requirement for it, and it may thus not show an even elimination. However, PARIS and SIKORA (1967) have had some success in measuring assimilation rates in an isopod using P^{32}, and comment on the fact that such β-emitters are even more efficiently used with small animals. For the assimilation studies the animals were fed for several days with the P^{32} contaminated food before elimination was measured with a view to reducing the error in the estimate. The worth of such an estimate also relies on the assumption that the rate of food assimilation is proportional to the rate of isotope assimilation.

6.2. Discussion

The data obtained for *Damaeus clavipes* are summarised in Table 7.

At 50—65% the assimilation efficiencies are rather high, but nonetheless closely match those of 40—70% estimated by HEALEY (1967) for the collembolan *Onychiurus procampatus* GISIN. Both the springtail and the mite are fungal feeders, and it seems reasonable to suppose that these high efficiencies result from the ingestion of a rich and easily assimilable diet. The figures are, however, much higher than those estimated for most other oribatids. ENGELMANN (1961) gives an overall figure of 20%, and WEBB (1969) quotes 15% for an unidentified species. BERTHET's (1964) figures is even lower at 12%, although this is for the macrophytophage *Steganacarus magnus*. However, MURPHY (1952, 1953), using a gravimetric method, suggests that some 50% of the food intake by *S. magnus* was egested, thus giving an assimilation efficiency of 50%. For certain panphytophages, J. O. M. THOMAS (pers. comm.) offers figures of 40—50%, and it may well prove that assimilation efficiencies vary consistently according to the feeding group to which the animal belongs. In the light of the meagre information at present available one might tentatively suggest that figures for assimilation efficiency are likely to be of the order: macrophytophages (10—15%), panphytophages (40—50%), microphytophages (50—65%).

Table 7 Summary of food processing at 15 °C by *Damaeus clavipes* adults and juveniles

	Amount ingested/ animal/day		Amount ingested/ μg d. wt. animal/day		% body dry weight ingested	% of radiophosphorus assimilated	Assimilation efficiency %	
	dry weight μg	calories	dry weight μg	calories			method 1	method 2
Protonymphs	0.39	0.00186	0.09	0.000430	9.0	64.1	63.3	—
Deutonymphs	0.72	0.00344	0.07	0.000334	7.0	62.8	65.7	—
Tritonymphs	1.49	0.00711	0.06	0.000286	5.5	50.4	46.7	—
Adults	5.80	0.02670	0.09	0.000414	9.0	63.8	61.5	62.7

The temperatures at which ENGELMANN and WEBB worked are not known. BERTHET's figures are based on experiments done at 18—22 °C, THOMAS's at about 20 °C, and MURPHYS at 4—5 °C. Assimilation efficiencies (as well as ingestion and egestion rates) will almost certainly vary with temperature, and it will enable more critical comparisons to be made in future if temperatures are quoted. Moreover, extrapolations to field conditions may be more trustworthy if working temperatures in the laboratory more nearly span those encountered naturally in the soil.

From the data presented in Table 7 it seems that there is little variation in assimilation efficiency between the developmental stages. Only the tritonymphs appear to have a significantly depressed efficiency.

During the course of the ingestion experiments an attempt was made to measure assimilation efficiency by a different route ("method 2" in Table 7). The intake rate had already been calculated and the experimental animals were retained on uncontaminated food whilst their faecal material was collected over a period of days. This was counted in the counter/ratemeter then dried and weighed. That portion of it which was highly radioactive was assumed to have originated from the original radioactive meal and thus to represent F in the production biology equation. By simple subtraction from the already calculated C, an estimate of assimilation could be found. For the adults this gave an assimilation efficiency of 62.7 % comparing very favourably with the 61.5 % measured from the elimination curve. However, for the juveniles this method was not at all successful because 24 hours of feeding were not sufficient. Presumably developing juveniles have a strong requirement for P much of which is assimilated in a short time from the meal and released slowly over the succeeding days. Thus the faecal material remained radioactive for a much longer period than could be accounted for simply by the "waste" radioisotope in the faeces. The animals in the first assimilation experiment were fed for several days upon contaminated food before elimination was plotted, and were thus more nearly in equilibrium with the radioisotope.

The ingestion rate for *Damaeus* is low relative to that measured for other oribatid mites. KOWAL (1969) estimates a consumption of 0.25 μg pine mor/μg mite/day for *Cultroribula juncta* (MICHAEL) at 20 °C; an intake, that is, of 25 % of the dry body weight/day. One might expect a reasonably high intake for an animal feeding on a relatively less easily assimilable material such as pine needles, but ENGELMANN (1961) estimates even higher (40 %) for oribatids feeding on yeast. Figures obtained in the current studies of between 5.5 and 9 % for *Damaeus clavipes* seem very low in contrast, but compare very well with those of MCBRAYER and REICHLE (1971) of 1.7 to 9 % dry body weight ingested/day for mycophages measured in the field. BERTHET's (1964) figures for the ingestion rate

Amount of food assimilated/animal/day (as % of intake)		Mean number of faecal/pellets egested/animal/day	Amount egested/ animal/day (by subtraction)		C = A + F (cals)
dry weight μg	calories		dry weight μg	calories	
0.25	0.00118	0.66	0.14	0.00068	0.00186 = 0.00118 + 0.00068
0.47	0.00226	2.40	0.25	0.00118	0.00344 = 0.00226 + 0.00118
0.70	0.00332	3.60	0.79	0.00379	0.00711 = 0.00332 + 0.00379
3.60	0.01640	0.84	2.20	0.01030	0.02670 = 0.01640 + 0.01030

of *Steganacarus magnus* are also low, with a mean of 4.4 μg dry weight of leaf material consumed/animal/day at 18 °C. For *Steganacarus magnus* the proportion of dry weight to fresh weight is 60 % so this amounts to an intake of only 2 % of the body weight/day. MURPHY (1952, 1953) quotes a figures of 3.5 μg/animal/day for *S. magnus* at 4—5 °C which represents an intake of about 1.5 % of the body weight/day. MCBRAYER and REICHLE (1971) quote a figure of 1 % for "Phthiracaridae". BERTHET has also noted a differential ingestion rate for *Steganacarus magnus* feeding on dead leaf material from different tree species. Thus the oribatid consumed some 4 % of its body weight/day when eating hazel and hornbeam, and some 2 to 3 % when eating oak and beech.

Comparisons of intake rate between developmental stages of the same species on the basis of % dry body weight ingested do not seem particularly valid in view of the fact that these stages progressively increase the amount of sclerotisation of their bodies. Table 7 also indicates ingestion rates on a per animal basis and this shows much more clearly the variation between the stages. On this basis it appears that the adults are able to process by far the most material. The tritonymphs make up for a poor assimilation efficiency by having a high ingestion rate, which is twice that of the deutonymphs and four times that of the protonymphs, thus effectively assimilating as much or more material/day in terms of calories/animal. However, the egestion rate for the tritonymph also appears to be very high when assessed from faecal pellet production, and this presumably accounts for the low assimilation efficiency. The high assimilation efficiency of the protonymphs and the adults would seem to be due to the longer retention of material in the gut, and that of the deutonymph perhaps to a greater efficiency of digestion.

Only HARTENSTEIN (1962f) appears to have timed the passage of food material through the gut of an oribatid mite. He observed the process in *Protoribates lophotrichus* which was fed upon decaying leaf material. Approximately two hours were required for the development of a food bolus in the ventriculus of the mite which moved, after a further two hours, to the colon. After residing in the colon for two more hours it passed to the rectum for a further two hour period. Only 8 hours elapsed therefore from the time of ingestion to that of defaecation. HARTENSTEIN (1962e) also estimated a gut residence time of some 8—9 hours for both fungus and dead leaf material in *Platynothrus peltifer*. Overall gut residence time for *Damaeus clavipes*, measured from radioisotope elimination curves (Figs. 1—4), was much longer; some five days for the adults, five days for the protonypmhs, seven days for the deutonymphs and eight days for the tritonymphs. From the ingestion experiments the bulk of the material was egested after five or six days for the adults and the juveniles. For the former the peak egestion period was between the third and fourth day, and for the latter between the second and third day. The longer gut residence time here measured may be something of an overestimate (since the progress

of more than one food bolus will have been plotted; since the temperature at which HARTENSTEIN's measurements were made, though not quoted, was almost certainly higher; and since the *Damaeus* figure results from a series of means), but nonetheless it is reasonable to suppose that the gut residence time is still substantially higher than that measured by HARTENSTEIN. Clearly this is the reason for the higher assimilation efficiency found in the microphytophages which will retain the relatively rich energy source for longer since more of it is assimilable. The macrophytophages, on other hand, may pass food material quickly because only faces exposed by them in their chewing will be readily digestible, and it would be advantageous to expose these to enzyme action at as great a rate as possible. HAYES (1963) has shown that *Euphthiracarus arduus* produces the maximum amount of faeces when feeding upon the most decayed leaf material, and *Steganacarus magnus* when feeding upon the middle stages of decay. Ordinarily one might suppose that this is in order to digest microbial growths but, since it has been suggested earlier in this paper that macrophytophages may not have the capacity to digest such growths, the faster food processing may reflect a difficulty on the part of the mite to find sufficient assimilable faces on the ingested material which have not already been utilised by the microflora.

The faster rate of food processing in macrophytophages and panphytophages may be better reflected in the rate of faecal pellet production. HARTENSTEIN (1962e, f) measured a mean daily egestion rate for *Platynothrus peltifer* and *Protoribates lophotrichus* of 8 pellets/individual, and for *Steganacarus magnus* BERTHET (1964) measured a mean of 6.5 pellets ejected/day at 22 °C. For *Damaeus clavipes* the greatest number (3.6/animal/day) are produced by the tritonymphs, and the least by the protonymphs and the adults (0.66 and 0.84 respectively). However, it must be noted that both MURPHY (1955) and HAYES (1963), measured a mean production of only 0.7 pellets/day for *Steganacarus magnus*, although HAYES indicates that this was from feeding on fresh litter and at a temperature of 19 °C. The above remarks on food gut residence times according to the availability of assimilable carbohydrates for the various feeding groups may thus be pertinent.

7. General discussion

Oribatid mites are probably the most abundant group of arthropods in most soils. Even though these mites are quite small (0.2 to 2 mm in length) their particular feeding habits fit them well for the role of secondary decomposers in the soil system, and they play an important part in the breakdown of plant residues. There are a variety of niches available to oribatids in the decomposing organic debris of the soil, and this is reflected in the varied structure of their mouthparts which may be suitable for dealing with woody material, the leaf lamina, bacteria, or fungal mycelia and spores.

BERTHET (1967) has pointed out that, on the basis of energy flow, the oribatids seem to play a much smaller role than some other edaphic animal groups. Their overall activity, at 30 Kcals/m²/year of energy released (BERTHET 1967; MACFADYEN 1964), is some 5 to 12 times less than that of nematodes and up to 5 times less than that of enchytraeids.

The amount of material they actually process, however, may be found to be somewhat higher than that usually assumed, in view of the figures presented in this paper for the ingestion rate and assimilation efficiency of a microphytophagous oribatid. Already it is thought that up to 50 % of the annual leaf fall may be passed through the gut of the oribatid populations (BERTHET 1964; COLEMAN 1970; RAJSKI 1966), but there is growing evidence that the panphytophagous oribatids process perhaps twice as much material as those macrophytophages on which BERTHET based his original estimate. It is not

possible at this stage to give positive figures for quantities of energy processed by the field populations of oribatids in Hestehave wood, but it is clear that any estimate must be based on data for each of the general feeding groups rather than on a misleading mean figure for oribatids as a whole.

The possible ecological role of oribatid mites in the soil system has been discussed many times before (BERTHET 1967; MACFADYEN 1964, 1968; WALLWORK 1967, 1970). The general consensus of opinion is that oribatid mites perform a role as secondary decomposers mainly by conditioning the organic debris for action by the primary decomposers, the microbial flora. To use MACFADYEN's word, they act as "catalysts". The macrophytophages and the panphytophages assist in the fragmentation of the organic debris and in so doing increase the surface area of this debris for further microbial colonisation and for the leaching of minerals by rainwater. It is also now clear that some oribatid mites may act as primary decomposers themselves with the ability to digest certain of the plant structural polysaccharides. How much of this material they hydrolyse is as yet an unanswerable question. It is conceivable that their digestive capability has a two-fold action; first providing assimilable material for their own nutrition and, second developing a more highly nutritive substrate for the rapid initiation of microbial colonies in the faecal material. This paper has shown that the macrophytophagous oribatids do not appear to possess an enzyme capable of digesting a most important fungal storage carbohydrate (trehalose), which is at least circumstantial evidence that they do not, as has previously been supposed, digest much of the microbial growth which is carried on their food. If this is the case then their activity as conditioning agents for the decomposition process is further enhanced since they will egest a more readily degradable product replete with a complement of viable microbes.

That living fungal spores and hyphae exist in the faecal material of certain oribatids is, in any case, clear (MIGNOLET in press, a). The oribatids in their movements through litter no doubt also act as dispersal agents for the microbial flora by conveying spores in their guts and on their body surfaces (MACFADYEN 1964, 1968), and WITKAMP (1960) has shown that they may disseminate fungal spores when introduced into sterile soil. Their specific fungal feeding patterns, shown in this paper, may cause them to enhance fungal growth simply by clearing away antibiotic-producing fungi. The voracious feeding of *Belba corynopus* on *Penicillium* spp., for instance, is probably of significance in allowing a greater opportunity for other decay fungi to grow. The very process of grazing microbial growths from litter (called "sanitation" by VAN DER DRIFT) may also stimulate attack by the next group of microbes in the succession (MACFADYEN 1964; VAN DER DRIFT 1965; MCBRAYER and REICHLE 1971).

Clearly there is a very close and complicated relationship between the soil microflora and the oribatid mites, which may be on several levels. The macrophytophages will not readily consume fresh litter material and require it to be somewhat decayed first. WALLWORK (1958) has raised the possibility that the feeding of these mites may be limited by the texture of the food material. If these animals do not digest the originators of decay in their food material then possibly the relationship between mite and microbe is indirect, the microflora merely acting, in its turn, as a physical conditioner for the litter, rendering it palatable to the mite (HAYES 1963; LITTLEWOOD 1969). On the other hand, macrophytophages may simply be attracted to older litter because weathering has leached away the unattractive water-soluble polyphenols (EDWARDS, REICHLE and CROSSLEY 1970). However, HARTENSTEIN (1962f) has shown that the panphytophage *Protoribates lophotrichus* will not continue to feed on decayed leaf material which has had its microbial flora destroyed. Presumably, then, in the case of the panphytophages the influence of microbes on the texture of dead leaves may be of little significance and, despite a generally wide range of carbohydrase enzymes, they may also require microbes as a dietary component.

The catholic feeding habits of the panphytophages may be of great ecological significance, allowing them to range through a variety of habitats as well as through most or many of the organic horizons capable of physically accommodating them. Even within this group, though, there may be certain restrictions, and animals such as *Achipteria coleoptrata* and *Chamobates cuspidatus* may be confined because of their feeding preferences to certain layers of the woodland floor. They would be unlikely, however, to be restricted to any particular woodland habitat.

It has been shown that microphytophagous and panphytophagous oribatid mites may be distributed vertically in the organic horizons according to their feeding preferences. This relationship is unlikely to be simple or direct, but for those animals with a very distinctive feeding specificity it may well be significant, for usually microbial growths precede colonisation by the fauna (Burges 1967), and the fauna may colonise soil according to the pattern of fungal development (Coleman and Macfadyen 1966; Macfadyen 1969). The close relationship between oribatids and their preferred food source is also of interest for the distinction shown between the developmental stages. There appears to be no competition between the juveniles and adults for resources since their feeding preferences are different and usually the preferred foods grow in different vertical layers.

Wallwork (1967) suggests that the oribatids are important in the deep mixing of material in woodland soils, and certainly they would render dead organic matter into fragments and faecal conglomerates small enough to be washed fairly swiftly through the leaf litter and into the humus and mineral layers where bacteria (which occur here in the greatest numbers) may continue the breakdown process. The importance of oribatids in this process is probably greatest in mor soils where earthworms are few and where mites reach their greatest abundance.

The experiments reported in this paper on food processing by microphytophagous mites indicate that the adult deals with by far the most material. Whether this remains significant after consideration of the field populations remains to be seen. Of the juvenile stages, the tritonymphs turn over the most material but assimilate least, and the deutonymphs appear to have the greater digestive efficiency. Webb (1969) has measured the respiratory metabolism of all the developmental stages of *Nothrus silvestris* and has indicated the importance of the juvenile metabolism (especially that of the protonymphs). Wallwork (1967) also makes the point that the weakly chitinised immatures are more vulnerable to predators and may therefore participate more than the adults in the transfer of material and energy to higher trophic levels. In future considerations of the role of oribatid mites on energy flow in ecosystems it is clear that more regard should be given to the immatures.

It is also clear that a fuller understanding of the feeding habits of soil oribatids is required in order to make a more cogent analysis of the role of these animals in the energetics of the ecosystem. Moreover, although measurement of energy flow remains the most readily applicable criterion with which to assess the relative importance of the various exploiter populations in an ecosystem, the real importance of their ecological effectiveness may well be found to occur in their indirect influence on the system through their particular behavioural idiosyncrasies.

A close study of the feeding behaviour of oribatid mites appears to be rewarding in this regard. The categorisation of feeding habits may also be of importance in future discussion but, as Wallwork (1970) says, distinction should be made between what is ingested and what is utilised. The revised nomenclature presented at the beginning of this paper goes some way towards this, and the use of the main categories in this classification when discussing the ecological influences, qualitative or quantitative, of oribatid mites in the soil may provide us with a closer approximation to reality than has hitherto been the case.

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9. Summary · Zusammenfassung

Information on the feeding biology of oribatid mites is summarised from the literature, and a list provided of the broad feeding preferences of various species. Descriptive nomenclature of oribatid feeding habits is revised and refined, and it is suggested that the ecological significance of soil oribatids may be much clarified if discussed in terms of the general feeding categories.

The feeding specificities of oribatids are dealt with in terms of original laboratory work on species from the soils of a Danish beech wood, as well as from information in the literature. It is shown that oribatids may have distinct preferences for consuming certain microbial species, a habit which may be important in terms of their distributions in the soil profile. All of the juveniles tested had different food preferences from their adults and for foods, moreover, which are found in different organic layers from those inhabited by their adults.

Information is provided about the carbohydrase enzymes possessed by some twelve species, of oribatids. It is clear that the litter-eaters possess enzymes capable of digesting certain plant structural polysaccharides such as cellulose, xylan, and pectin. The macrophytophages do not have a trehalase, suggesting that they do not, after all, digest much of the microbial growth on their food material.

Assimilation efficiencies and ingestion and egestion rates are estimated at 15 °C for protonymphs, deutonymphs, tritonymphs and adults of *Damaeus clavipes* using radioisotopes. Assimilation efficiencies are high at 60—65 % for all stages except the tritonymph for which it is 50 %. It is suggested that figures for assimilation efficiency may be of the order: macrophytophages, 10—15 %; panphytophages, 40—50 %; microphytophages, 50—65 %. Intake rates for *D. clavipes* are between 5.5 and 9 % of dry body weight ingested/day, and compare favourably with those measured for mycophages in the field. A discussion of the ecological importance of soil oribatids concludes the paper.

[Untersuchungen von Oribatiden eines dänischen Buchenwaldes]

Es werden Informationen über die Ernährungsbiologie von Oribatiden zusammenfassend dargestellt, und es wird eine Liste mit einer Übersicht über die weiten Nahrungspräferenzen von verschiedenen Arten dargeboten. Die deskriptive Nomenklatur der Ernährungsgruppen der Oribatiden wurde revidiert und die Begriffe wurden neu definiert. Es wird darauf verwiesen, daß die ökologische Bedeutung der Oribatiden vielleicht verdeutlicht werden würde, wenn man sie unter Berücksichtigung der Ernährungsgruppen diskutierte.

Die hier erwähnten Ernährungsgruppen basieren sowohl auf der Erfahrung aus eigener Laboratoriumsarbeit mit Arten aus einem dänischen Buchenwald als auch auf Literaturinformationen. Es wird gezeigt, daß Oribatiden bestimmte Präferenzen beim Konsum gewisser Mikroben haben können, ein Verhalten, das für ihre Verteilung im Bodenprofil von Bedeutung sein kann. Alle getesteten Juvenilen hatten in Vergleich zu ihren Adulten unterschiedliche Nahrungspräferenzen, insbesondere jene, die in anderen organischen Bodenschichten vorkommen als die Adulten.

Carbohydrasen wurden bei 12 Oribatiden-Arten gefunden. Es ist klar, daß die Blattfresser Enzyme besitzen, die ihnen die Verdauung gewisser pflanzlicher struktureller Polysaccharide, wie Cellulose, Xylan und Pektin, ermöglicht.

Die Makrophytophagen haben keine Trehalase, was darauf hindeutet, daß sie, nach allem was bisher bekannt ist, viel vom Mikrobenaufwuchs ihres Nahrungsmaterials verdauen.

Mit Hilfe von Radioisotopen wurden für Proto-, Deuto- und Tritonymphen sowie für Adulti von *Damaeus clavipes*, bei einer Temperatur von 15 °C, Assimilationsraten sowie Raten der Nahrungsaufnahme und Kotabgabe ermittelt. Die Assimilationsraten sind mit 60—65 % für alle Stadien (mit Ausnahme der Tritonymphen, bei denen sie nur 50 % betragen) hoch. Es wird darauf verwiesen, daß die Assimilationsraten folgende Größenordnung haben mögen: Makrophytophage (10—15 %), Panphytophage (40—50 %), Mikrophytophage (50—65 %). Die Raten der täglichen

Nahrungsaufnahme lagen bei *D. claviges* zwischen 5,5 und 9,0 % des Körper-Trockengewichts und entsprechen somit jenen Raten, die im Freiland für Mikrophytophage ermittelt wurden. Eine Diskussion über die ökologische Bedeutung der Boden-Oribatiden beschließt die Darstellung.

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11. Appendix · Main feeding prereferences of oribatid mites

11.0. Prefatory note

* = not representative of a preference experiment.
mac = reported in relevant paper as a macrophytophage.
mic = reported in relevant aper as a microphytophage.
pan = reported in relevant paper as a panphytophage.
( ) = reported in relevant paper as a potential but generally unsatisfactory feeding habit for the adults, or as a feeding habit of a juvenile stage only.

11.1. Macrophytophages

Cepheidae: *Cepheus la us* C. L. Koch 1836. Wallwork 1958.
Euphthiracaridae: *Euphthiracarus arduus* (C. L. Koch 1841). Murphy 1955.*, Hartenstein 1962a, pan.
Euphthiracarus monodactylus (Willmann 1920). Schuster 1956.
Oribotritia cribaria (Berlese 1904). Schuster 1956.
Oribotritia decumana (C. L. Koch 1836). Schuster 1956.
Oribotritia loricata (Rathke 1799). van der Drift 1951, Riha 1951. Schuster 1956, Hayes 1963*.
Hermanniellidae: *Hermanniella granulata* (Nicolet 1855). Noordam and de Vlieger 1943* Riha 1951. Schuster 1956.
Mesoplophoridae: *Mesoplophora pulchra* (Sellnick 1928. Wallwork 1958.
Perlohmanniidae: *Perlohmannia dissimilis* (Hewitt 1908). Schuster 1596.
Phthiracaridae: *Phthiracarus borealis* (Träghårdh 1910). Noordam and de Vlieger 1943*. Van der Drift 1951. Wallwork 1958.
Phthiracarus boresetosus Jacot 1938. Jacot 1939*.
Phthiracarus italicus (Oudemans 1906). Wallwork 1958.
Phthiracarus ligneus Willmann 1931. Noordam and de Vlieger 1943*. Riha 1951.
Phthiracarus piger (Scopoli 1763). Noordam and de Vlieger 1943*. Hayes 1963*.
Phthiracarus setosellum Jacot 1929. Hartenstein 1962a, pan.
Steganacarus applicatus (Sellnick 1920). Schuster 1956.
Steganacarus clavigerus (Berlese 1904). Schuster 1956.
Steganacarus diaphanum Jacot 1930. Wallwork 1958. Hartenstein 1962a, g, (pan?).
Steganacarus laevigatus (C. L. Koch 1844). Schuster 1956.
Steganacarus magnus (Nicolet 1855). Murphy 1952, 1953, 1955*. Wallwork 1958. Hayes 1963*. Luxton.

Steganacarus phyllophorus (Berlese 1904). Schuster 1956.
Steganacarus spinosus (Sellnick 1920). Luxton
Steganacarus thoreaui (Jacot 1938). Jacot 1939*.
Tropacarus carinatus (C. L. Koch 1841). Riha 1951.
Tropacarus pulcherrimus (Berlese 1884?). Riha 1951. Schuster 1956.

11.2. Microphytophages

Amerobelbidae: *Amerus troisii* (Berlese 1883). Schuster 1956.
Ameronothridae: *Hygroribates schneideri* (Oudehans 1905). Luxton 1966.
Damaeidae: *Belba compta* (Kulczynski 1902), Forsslund 1939*. Schuster 1956.
Belba corynopus (Hermann 1804). Schuster 1956. Luxton.
Belba gracilipes Kulczynski 1902. Pauly 1952.
Belba kingi Hartenstein 1962. Hartenstein 1962a, b.
Belba meridionalis Bulanova-Zachvatkina 1962. Šerif 1971.
Belba minutissima (Sellnick 1920). van der Drift 1951.
Belba riparia (Nicolet 1855). Schuster 1956.
Belba tatrica (Kulczynski 1902). Schuster 1956.
Belba verticillipes (Nicolet 1855). Schuster 1956.
Damaeus auritus (C. L. Koch 1836). Schuster 1956.
Damaeus clavipes (Hermann 1804). Pauly 1952.
Schuster 1956. Luxton.
Damaeus geniculosus (Oudemans 1929). Pauly 1952.
Damaeus onustus C. L. Koch 1841. Littlewood 1969*.
Mignolet, in press, a.
Epidamaeus kamaensis (Sellnick 1925). Šerif 1971.
Metabelba montana (Kulczynski 1902). Hartenstein 1962a, c.
Metabelba pulverulenta (C. L. Koch 1840). Schuster 1956.
Riha 1951, (necro.)
Porobelba spinosa (Sellnick 1920). Littlewood 1969*.
Eremaeidae: *Eremaeus hepaticus* C. L. Koch 1836. Schuster 1956.
Eremobelbidae: *Eremobelba nervosa* Hartenstein 1962. Hartenstein 1962a, c.
Gustaviidae: *Gustavia microcephala* (Nicolet 1855). Schuster 1956. Luxton.
Gymnodamaeidae: *Gymnodamaeus bicostatus* (C. L. Koch 1836). Schuster 1956.
Hypochthoniidae: *Hypochthonius rufulus* C. L. Koch 1836. Riha 1951 (necro). Hartenstein 1962a. Farahat 1966*. Luxton.
Metrioppiidae: *Ceratoppia bipilis* (Hermann 1804). Hartenstein 1962a. Littlewood 1969* (necro).
Ceratoppia quadridentata (Haller 1880). Schuster 1956.
Ceratoppia sexpilosa Willmann. Schuster 1956.
Mycobatidae: *Punctoribates quadrivertex* (Halbert 1920). Luxton 1966.
Oppiidae: *Oppia concolor* C. L. Koch 1844. Šerif 1971.
Oppia neerlandica (Oudemans 1900). van der Drift 1951. Wallwork 1958, pan? Woodring and Cook 1962*.
Oppia nitens C. L. Koch 1836. Farahat 1966*. Sengbusch and Sengbusch 1970*.
Oppia nova 1902). Hartenstein 1962a, Lebrun 1970, Woodring 1963 (necro).
Oppia subpectinata (Oudemans 1901). Schuster 1956.
Tectocepheidae: *Tectocepheus velatus* (Michael 1880). Riha 1951.
Wallwork 1958?. Kühnelt 1961.
Trhypochthoniidea: *Trhypochthonius tectorum* (Berlese 1896). Schuster 1956.

11.3. Panphytophages

Achipteriidae: *Achipteria coleopterata* (Linnaeus 1758). Wallwork 1958, pan. Farahat 1966, *mic. Luxton, pan. Noordam and de Vlieger 1943, *mac.
Parachipteria punctata (Nicolet 1855). Forsslund 1939, *pan.
Camisiidae: *Camisia segnis* (Hermann 1804). Forsslund 1939, *mic. Schuster 1956, pan. Littlewood 1969, *mic.
Camisia spinifer (C. L. Koch 1835), Schuster 1956, pan. Hartenstein 1962a, pan. Noordam and de Vlieger 1943, *mac. Littlewood 1969, *mic.

Heminothrus paolianus Berlese 1913. Forsslund 1939, *mic.
Platynothrus peltifer (C. L. Koch 1840). Schuster 1956, pan. Hartenstein 1962a, e, pan. Berthet 1964, mic. Littlewood 1969, *mic. Noordam and de Vlieger 1943, *pan.
Carabodidae: *Carabodes areolatus* Berlese 1916. Schuster 1956, pan. Hartenstein 1962a, pan.
Carabodes coriaceus C. L. Koch 1836. Noordam and de Vlieger 1943, *mac.
Carabodes femoralis (Nicolet 1855). Riha 1951, mic. Kühnelt 1961, mic.
Odontocepheus elongatus (Michael 1879). Littlewood 1969, *mic.
Ceratozetidae: *Ceratozetes cisalpinus* Berlese 1908. Woodring and Cook 1962, *mic.
Ceratozetes gracilis (Michael 1884). Hartenstein 1962a, d, pan. Luxton, pan.
Ceratozetes jeweli Rockett and Woodring 1966. Rockett and Woodring 1966b, *mic.
Fuscozetes fuscipes (C. L. Koch 1844). Wallwork 1958, pan (necro).
Chamobatidae: *Chamobates cuspidatus* (Michael 1884). Luxton, pan.
Chamobates schützi (Oudemans 1901). van der Drift 1951, mic.
Euzetidae: *Euzetes globulus* (Nicolet 1855). Berthet 1964. mic. Mignolet in press, a, mic.
Euzetes seminulum (Müller 1776). Schuster 1956, pan.
Galumnidae: *Galumna confusa* Woodring 1965. Woodring 1963, *mic. Woodring 1965, *mic. Sengbusch 1954, *pan.
Galumna cf. *dorsalis* (C. L. Koch 1841). van der Drift 1951, mic.
Galumna elimata (C. L. Koch 1841). Hartenstein 1962a, mic.
Galumna formicarius (Berlese 1914). Wallwork 1958, mic?.
Galumna longipluma (Berlese 1904). Sengbusch 1954, *pan.
Galumna minutus (Ewing 1909) Woodring 1963, *mic.
Galumna parva Woodring 1965. Woodring 1965, *mic.
Orthogalumna? terebrantis Wallwork 1965 (?Wallwork). Wallwork 1965, *mac.
Pergalumna nervosa (Berlese 1914). Sengbusch 1954, *pan.
Pergalumna omniphagous Rockett and Woodring 1966, Rockett and Woodring 1966a, b, *mic (zoophag).
Haplozetidae: *Rostrozetes flavus* Woodring 1965. Woodring 1965, pan.
Hermanniidae: *Hermannia gibba* (C. L. Koch 1840). Murphy 1952, *mac. Schuster 1956, pan. Hartenstein 1962a, pan. Noordam and de Vlieger 1943, *mac.
Hermannia pulchella Willmann 1952. Luxton 1966, mic.
Liacaridae: *Adoristes ovates* (C. L. Koch 1840). Forsslund 1939, *pan. Littlewood 1969, *mic. Luxton, pan.
Liacarus coracinus (C. L. Koch 1841). Noordam and de Vlieger 1943, *mac.
Liacarus tremellae (Linnaeus 1761). Schuster 1956, pan. Farahat 1966, *mic.
Liacarus xylariae (Schrank 1803). Riha 1951, mac. Kühnelt 1961, *mac.
Liodidae: *Liodes farinosus* (C. L. Koch 1840). Schuster 1956, pan.
Platyliodes scaliger (C. L. Koch 1840). Schuster 1956, pan.
Nanhermanniidae: *Nanhermannia elegantula* Berlese 1913. Schuster 1956, pan. Hartenstein 1962a, pan.
Nanhermannia nana (Nicolet 1855). Forsslund 1939, *mic.
Nothridiae: *Nothrus biciliatus* C. L. Koch 1844. Hartenstein 1962a, pan.
Nothrus palustris C. L. Koch 1840. Schuster 1956, pan. Lebrun 1956, pan. Luxton, pan. Mignolet 1971, a, mac.
Nothrus pratensis Sellnick 1928. Tarras-Wahlberg 1961, *mic.
Nothrus silvestris Nicolet 1855. Noordam and de Vlieger 1943, *mac. van der Drift 1951, *mac. Schuster 1956, pan. Luxton, pan.
Oribatulidae: *Hemileius initialis* (Berlese 1908). Forsslund 1939, *mic. Luxton, pan? (necro)
Oribatula minuta (Banks). Hartenstein 1962a, mic.
Oribatula tibialis (Nicolet 1855). van der Drift 1951, mic.
Protoribates lophotrichus (Berlese 1904). Hartenstein 1962a, f, pan (cop).
Scheloribates laevigatus (C. L. Koch 1836). Wallwork 1958, cop? Woodring and Cook 1962, mic*.
Scheloribates nudus Woodring 1965. Woodring 1965. pan.
Scheloribates pallidulus (C. L. Koch 1840), Wallwork 1958, pan. Hartenstein 1962a, mic.
Scheloribates parabilis Woodring 1965. Woodring 1965, pan (necro).
Xenillidae: *Xenillus anasillus* Woolley 1966. Luxton, pan.
Xenillus tegeocranus (Hermann 1804). Schuster 1956, pan. Berthet 1964, mic.
Zetorchestidae: *Zetorchestes micronychus* (Berlese 1883). Schuster 1956, pan.